

Adventitious Rooting in 'Hopi' Sunflower: Function and Anatomy¹

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ABSTRACT

The 'Hopi' sunflower (*Helianthus annuus* L.) is a primitive open-pollinated variety that produces numerous adventitious buds (nodules) on exposed lower stalks under greenhouse conditions. Similar conditions do not induce such budding in more advanced hybrids. The root buds remain dormant when exposed to air, but begin rapid growth into adventitious roots when covered with damp soil. Objectives of this study were to determine the effects of adding basal soil around stalks of Hopi and hybrid '894' sunflower on adventitious root development, contribution of the roots to plant standability, and anatomy of the roots. The addition of one or two 100-mm layers of soil around lower stalks induced significantly more (1% level) adventitious root growth above the original soil level on stalks of Hopi variety than on hybrid 894 stalks. When the addition of soil was delayed until plants were flowering, extensive adventitious rooting still occurred in Hopi sunflower, but little occurred in hybrid 894. Applying horizontal forces to stalks 0.3 and 0.6 m above the original soil level caused significantly less stalk deflection in Hopi than in hybrid 894 plants. The greater resistance to stalk deflection in Hopi was attributed to greater plant stability furnished by more extensive adventitious rooting. Anatomical studies revealed that the internal anatomy of adventitious roots was nearly identical to the internal anatomy of primary roots for both Hopi and hybrid 894. Roots of hybrid 894 had larger intercellular spaces in the cortex and a higher xylem to cortex ratio than comparable roots of the Hopi variety.

Additional index words: *Helianthus annuus* L., Drought resistance, Plant stability, Cropping practices, Compositae.

ADVENTITIOUS roots are distinguished from primary roots by their origin. Primary roots originate from the root pole of the embryo, whereas adventitious roots originate endogenously or develop in the vicinity of vascular tissue on aerial and underground stems and on old roots of plants (Esau, 1965). Adventitious roots may be complementary to primary root systems and may function in plant anchorage and in water absorption and conduction. The entire root systems of corn (*Zea mays* L.), other grain crops, and most grasses are essentially adventitious and conductive (Luxova and Kozinka, 1970; Taylor and Klepper, 1978). Many species of dicots also produce adventitious roots but their function is less clear than in monocots (Esau, 1965). Several studies have dealt with the role of flooding in inducing adventitious rooting in cultivated sunflower (*Helianthus annuus* L.) (Jackson, 1955; Kawase, 1972; Kawase and Whitmoyer, 1980; Kramer, 1951; Phillips, 1964; Stevenson and Boersma, 1964a, 1964b; Wample and Reid, 1975, 1978). Most of these studies dealt with the deleterious effects of flooding on sunflower associated with the development of adventitious roots.

The 'Hopi' sunflower is a primitive open-pollinated variety that originated and continues to be cultivated by the Hopi Indian Tribe in the semiarid southwest (Nabhan, 1979). It produces dormant adventitious root

buds (or nodules) under greenhouse conditions. Several other primitive, cultivated sunflower varieties (Stevenson and Boersma, 1964a, 1964b; Wample and Reid, 1975, 1978); some primitive breeding lines; and some wild *Helianthus* species [e.g., *H. niveus* spp. *tephrodes* (Gray) Heiser] also produce the adventitious root buds under greenhouse conditions. Similar conditions do not induce such budding in more advanced hybrids or breeding lines. For example, in an earlier greenhouse test, Hopi plants had an average of 37.1 ± 4.7 adventitious root buds on the lower stalks (Fig. 1), while adjacent hybrid '894' (cms HA 89 \times RHA

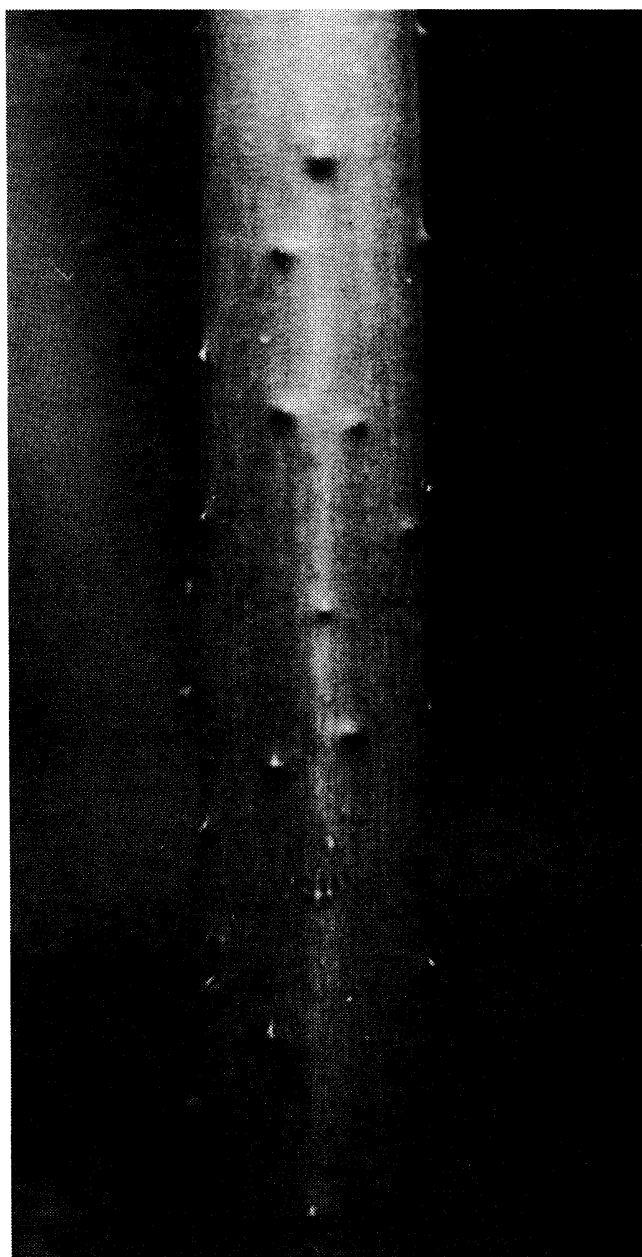


Fig. 1. Adventitious root buds (nodules) on exposed lower stalk of the 'Hopi' sunflower in the greenhouse.

¹ Contribution from USDA, ARS, Bushland, TX 79012, and The Kansas Agric. Exp. Stn. (Contribution No. 83-241-J), Kansas State Univ., Manhattan, KS 66506. Received 27 June 1983. Published in *Agron. J.* 76:429-434.

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274) plants had an average of 1.4 ± 0.4 buds (Fig. 2). Of the plants examined, a Hopi plant had a maximum of 86 adventitious root buds compared with a maximum of three on a hybrid 894 plant (unpublished data). Also, in furrow-irrigated field plots at Bushland, Tex., in the summer of 1980, 85% of Hopi plants contained adventitious root buds on the lower stalks, compared with only 5% for hybrid 894. Hence, it appears that the expression of adventitious rooting in sunflower has a genetic basis, as well as being environmentally induced as earlier reported (Jackson, 1955; Phillips, 1964; Stevenson and Boersma, 1964a). Adventitious root buds apparently remain dormant in sunflower when exposed to the air. However, once the buds become covered with moistened soil, adventitious root growth commences and proceeds rather rapidly, resulting in extensive rooting above the original soil layer (Fig. 3). The objective of this research was to study the effect of adding basal soil to stalks of Hopi and hybrid 894 sunflower on (1) adventitious root development, (2) the contribution of adventitious roots to plant standability, and (3) the anatomy of adventitious roots.

MATERIALS AND METHODS

Seed of Hopi and hybrid 894 sunflower were planted in 0.31-m diam greenhouse pots containing about 9.5 kg of air-

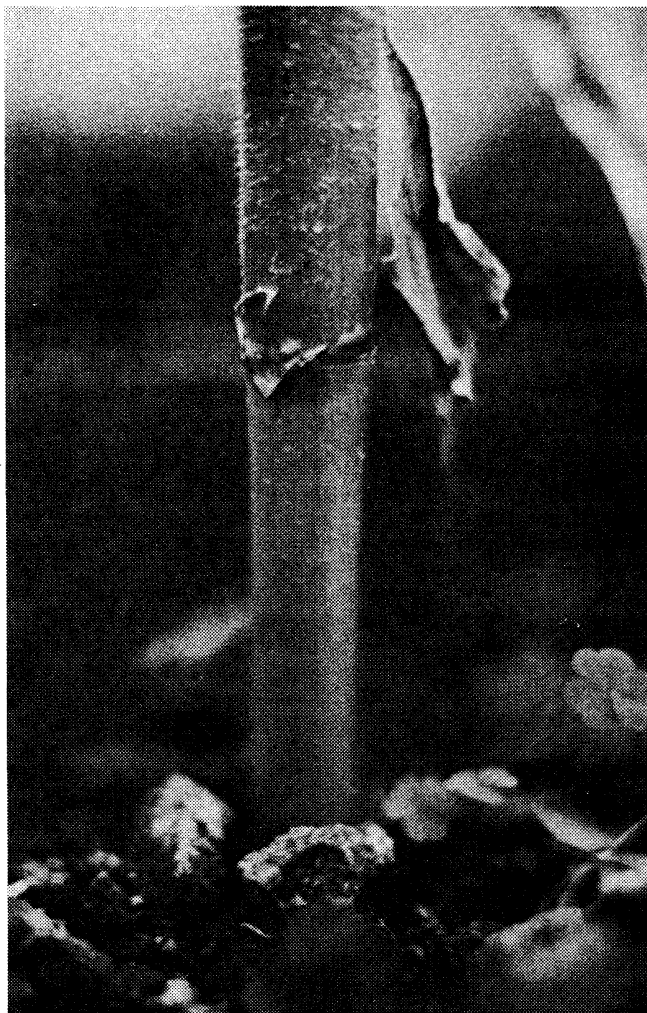


Fig. 2. Lower stalk of hybrid '894' sunflower lacking adventitious root buds under greenhouse conditions that induced budding on 'Hopi' sunflower shown in Fig. 1.

dry soil obtained from the surface horizon of Pullman clay loam (fine, mixed, thermic Torric Paleustolls). The pots were arranged in two rows in large greenhouse pans that provided uniform water absorption from the bottom of the pots as water was added to the pans. Water was added as needed to maintain vigorous plant growth. Hybrid 894 and Hopi sunflower were kept in separate pans to prevent excessive shading of hybrid 894 by the faster-growing, taller Hopi plants. Otherwise, all plants were handled uniformly throughout the study. After becoming established, the plants were thinned to one plant/pot, and randomly assigned soil-addition treatments. Within cultivars, plants for treatment were selected for uniformity of seedling vigor from a larger group of plants.

To study the development of adventitious roots, various quantities of soil were placed around the base of plants at different stages of development. Soil treatments began on Day 44 after planting when the Hopi plants averaged 0.75 m tall and hybrid 894 plants averaged 0.55 m tall. Treatments were: (1) no soil added (check), (2) 100 mm soil added on Day 44, (3) 200 mm soil added on Day 44, (4) 100 mm soil added on Day 44 and an additional 100 mm soil added on Day 58, (5) 100 mm soil added on Day 58, (6) 200 mm soil added on Day 58, and (7) 200 mm soil added at the start of anthesis, which was Day 77 for hybrid 894 and Day 94 for Hopi. The additional soil was placed within open-ended tar paper cylinders (300 mm in diameter and tall enough to contain the added soil) resting on the original soil surface apposed to the inner surface of pot rims. Treatments were replicated twice for hybrid 894 and three times for Hopi.

At physiological maturity (golden-yellow receptacles with bracts turning brown) (Schneider and Miller, 1981), plants were decapitated to about 1 m above the initial soil level for ease of handling. To estimate the effects of adventitious roots on plant standability, stalk deflections caused by horizontal forces of 0.45, 0.91, 1.4, 1.8, and 2.3 kg were measured. Force was applied against the stalks by a push-pull gauge at 0.3 and 0.6 m above the initial soil surface. At each height, the respective force was applied in turn from three directions.

Following the deflection measurements, soil was washed from the roots of each plant. Primary root length was measured, and the number of adventitious roots produced in each soil layer was counted. Roots were removed and oven-dried at 70°C for 24 h to determine the dry weight for roots developed in the different soil layers.

Internal anatomy of primary and adventitious roots was studied by removing primary rootlets and adventitious roots from Hopi and hybrid 894 prior to drying and preparing them for microscopic anatomical examination. The roots were kept moist with wet paper towels until short, cylindrical sections of the roots were removed and fixed in a 4% solution of cacodylate buffered glutaraldehyde, followed with buffer rinses and postosmification in 2% cacodylate buffered osmium tetroxide. Dehydrated root pieces were embedded in plastic resin, serially sectioned with glass knives in an ultratome at 1 to 2 μ m, and stained with toluidine blue for light microscopic observation.

Data for plant and rooting characteristics were analyzed by an analysis of variance and significantly different means within a cultivar were separated by Duncan's Multiple Range Test. Treatment means for the cultivars were compared by a paired *t*-test. Associations of stalk deflections due to a horizontal force and stem and root factors were analyzed by the multiple linear regression technique (Steel and Torrie, 1980).

RESULTS AND DISCUSSION

Data regarding effects of soil coverage on adventitious root growth in greenhouse-cultured sunflower are summarized in Table 1. As expected, adventitious roots did not develop in either cultivar where no soil was added subsequent to plant emergence. Also, the addition of soil following plant emergence had no sig-

nificant effect (5% level) on plant height or primary root development, although both mean plant height and mean primary root length were significantly greater (1% level) in Hopi than in hybrid 894 (Table 1). The extent of adventitious rooting that occurred in hybrid 894 following the addition of soil was unexpected because of the limited "budding" that occurs on this

cultivar with exposed stalks. However, the number of adventitious roots that developed was statistically similar for all treatments for which soil was added. Wample and Reid (1975) suggested that adventitious rooting may be induced by soil water in excess of field capacity around the roots of some sunflower cultivars. Although extra watering before weekends may have

Table 1. Plant and root characteristics for hybrid '894' and 'Hopi' sunflower due to the addition of basal soil.

Cultivar	Soil treatment†	Plant height	Primary root length	Adventitious roots in		Weight of dried roots		
				1st layer added soil	2nd layer added soil	Primary	Adventitious	
							1st soil layer	2nd soil layer
		m	cm	no.		g		
Hybrid '894'	1	2.1 a*	31 a	--	--	3.7 a	--	--
	2	2.2 a	9 a	20 a	--	1.3 a	0.3 a	--
	3	2.1 a	13 a	21 a	--	0.4 a	0.4 a	--
	4	2.2 a	17 a	22 a	0	1.9 a	0.4 a	0
	5	2.1 a	14 a	13 a	--	1.7 a	0.1 a	--
	6	2.1 a	14 a	14 a	--	0.9 a	0.3 a	--
	7	2.1 a	7 a	9 a	--	3.3 a	0.0 a	--
	Mean**	2.1	15	17	--	1.9	0.2	--
'Hopi'	1	2.7 a	52 a	--	--	4.1 a	--	--
	2	2.7 a	45 a	36 b	--	5.2 a	4.7 a	--
	3	2.9 a	36 a	93 a	--	2.5 a	3.2 a	--
	4	2.7 a	44 a	36 b	25	5.9 a	2.7 a	0.4
	5	2.6 a	34 a	48 ab	--	4.7 a	2.9 a	--
	6	3.0 a	31 a	65 ab	--	3.1 a	2.4 a	--
	7	2.3 a	32 a	61 ab	--	5.1 a	1.3 a	--
	Mean**	2.7	39	57	--	4.4	2.9	--

* Means for a cultivar followed by the same letter are not significantly different at the 5% level, by Duncan's Multiple Range Test.

** Means for Hopi are significantly different from the means for 894 at the 1% level, by a paired *t*-test.

† Treatments: 1 = no added soil (check); 2 = 100 mm soil added Day 44; 3 = 200 mm soil added Day 44; 4 = 100 mm soil added Day 44 + 100 mm soil added Day 58; 5 = 100 mm soil added on Day 58; 6 = 200 mm soil added Day 58; 7 = 200 mm soil added at flowering.



Fig. 3. 'Hopi' sunflower showing adventitious root development on the lower stalk where soil had been added above the original soil surface. (Note undeveloped buds above where soil line had been.)

caused some high soil water contents, the soil water content should not have exceeded field capacity because the water was added from the bottom.

The maximum number of adventitious roots developed in Hopi sunflower when 200 mm of soil were placed around the basal stalks on Day 44 after planting (Table 1). This treatment resulted in the development of significantly more (5% level) adventitious roots than occurred with Treatments 2, for which 100 mm of soil was added on Day 44, and with Treatment 4, for which 100 mm was added on Day 44 and 100 mm on Day 58. The number of adventitious roots averaged significantly greater (1% level) for Hopi than for hybrid 894. Soil treatments had no significant effects on dry weight of either primary or adventitious roots within cultivar, but the mean weights were significantly higher (1% level) for Hopi than for 894 (Table 1).

Fundamental questions remain unanswered concerning the evolutionary and adaptive value of adventitious rooting in sunflower. If adventitious roots of sunflower are conductive, as the adventitious roots of most dicots appear to be (Esau, 1960), why should flooding induce their development? Under conditions of excess water, sunflower would probably have little use for additional conductive roots. Indeed, Wample and Reid (1978) reported that adventitious roots in sunflower cultivars make no apparent contribution to the survival of flooded plants. Other studies have shown that extended flooding may cause hypertrophy of primary roots and the hypocotyl, in which cases there is circumstantial evidence that adventitious roots may contribute to plant recovery and survival following flood conditions (Kramer, 1951; Jackson, 1955). Several physiological and biochemical changes that occur in plants during periods of flooding are thought to contribute to the development of adventitious roots (Phillips, 1964; Wample and Reid, 1975). However, none of the characteristics normally associated with plant flooding, e.g., wilting of leaves, reduced shoot growth, epinastic curvature of leaves, chlorosis of lower leaves, or lower stem thickening (Phillips, 1964) was noticed in this study.

If flooding is a primary factor inducing adventitious rooting in sunflower as several authors have suggested, why should adventitious rooting be so pronounced in Hopi sunflower and wild species that have evolved in sandy soils of the semiarid and arid southwest (Heiser et al., 1969; Rogers et al., 1982) where flooding may rarely be a threat to survival? We suggest that adventitious rooting in primitive sunflower varieties and wild species may have adaptive value for survival in perennially droughty habitats, and that forced development of adventitious roots under artificial laboratory flood conditions may be only incidental to its real evolutionary significance. Many species of plants [such as, *H. niveus* Benth. (Brandegge)] inhabiting xeric environments routinely develop adventitious roots as a drought-resistance mechanism. In fact, the survival of blue grama grass [*Bouteloua gracilis* (H.B.K. Lag, ex Steud)] is clearly dependent upon its ability to extend adventitious roots into moist soil following rain (Wilson et al., 1976). Shallow roots radiating near the soil surface are able to take advantage of light rains, and conduct water that may otherwise be unavailable to

plants (Taylor and Klepper, 1978).

The tap root of some annual sunflowers may penetrate and extract soil water to depths of 2.5 to 3 m (Jones, 1978). Hence, if sufficient surface soil water is available to promote vigorous seedling growth, the tap root of sunflower has the ability to extract deeper soil water and maintain the plant until subsequent seasonal precipitation may occur (Weaver, 1926). It is during the latter growth stages that adventitious roots may be of maximum usefulness to sunflower, both as water conductors and as plant anchors. Ontogenetically, this is when adventitious root buds become most prominent on Hopi sunflower in the greenhouse (corresponding with floral bud development stage, ac-

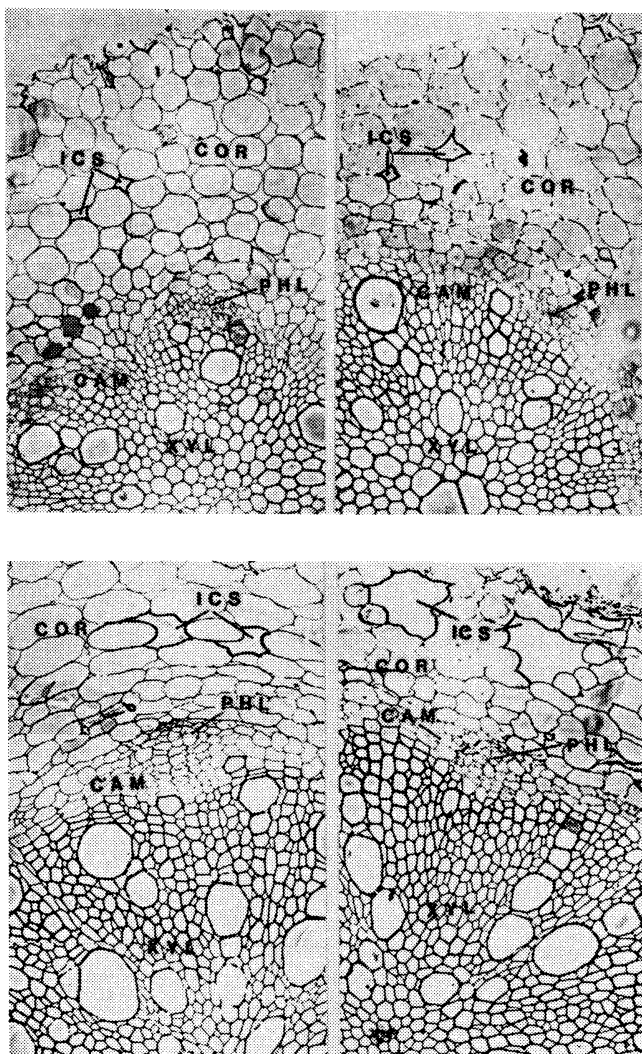


Fig. 4. Cross sections, at comparable levels of branching, of primary roots and adventitious roots of 'Hopi' and hybrid '894' sunflower. Water conducting xylem (XYL) and strands of sugar conducting phloem (PHL) are separated by dividing cells of the vascular cambium (CAM) adding growth to the root. Large cells in the xylem are vessels. Outside the phloem and cambium is a cortex (COR) of more or less compact parenchyma tissue, depending on the amount of intercellular space (ICS, ink-lined for clarity) (X 142). Top left. Hopi primary root. Top right. Hopi adventitious root. Lower left. Hybrid 894 primary root. Lower right. Hybrid 894 adventitious root.

Table 2. Summary of multiple linear regression analyses associated stem deflections at a 0.3-m height of hybrid '894' and 'Hopi' sunflower with sunflower stem and root factors, and depth of added soil. Deflections resulted from a horizontal force applied at the 0.3-m height.†‡

		Independent variables						
Dependent variable	Intercept	Stem diameter	Root length§	Dry weight of primary roots	Dry weight of adventitious roots	Added soil	SE†	R#
		cm		g		cm		
		Equation coefficients††						
894 - 0.9 kg force	3.495	--	--	--	--	-0.165(1)**	0.899	0.822**
894 - 1.8 kg force	8.782	--	--	--	--	-0.412(1)**	2.090	0.841**
Hopi - 0.9 kg force	10.816	-3.588(2)*	--	--	--	-0.192(1)**	1.556	0.773**
Hopi - 1.8 kg force	2.660	--	0.010(3)*	--	-0.176(2)**	-0.114(1)**	0.376	0.949**
894 + Hopi - 0.9 kg force	3.908	--	--	--	--	-0.197(1)**	1.412	0.724**
894 + Hopi - 1.8 kg force	6.477	--	--	-0.326(2)*	--	-0.254(1)**	1.808	0.741**

† Rankings are based on standardized regression coefficients and are shown in parentheses immediately after equation coefficients. Rankings are 1 (highest) and 3 (lowest).

‡ Levels of significance of equation coefficients are based on the *t*-test of the partial regression coefficients. Levels of significance are shown after rankings and are ** (1%) and * (5%).

§ Based on total length of major primary and adventitious roots.

† Standard error of estimate.

Coefficient of correlation. Level of significance was ** (1%).

†† Results are shown only for the analyses for which the partial regression coefficients were significant.

cording to Schneider and Miller, 1981). Also, in many dicots, adventitious budding coincides with primary root shrinkage that occurs shortly after maximum elongation of primary roots (Esau, 1965). It appears that these changes in primary roots would occur in sunflower about the time of floral bud growth, where biomass production in vegetative structures become less important in lieu of greater emphasis on producing reproductive biomass. Under cultivation, the most critical period for water needs in sunflower occurs during flowering and seed maturation (Unger, 1978), which under natural conditions might correspond with maximum adventitious root development.

Under natural conditions, adventitious root buds would probably have to become covered and subsequently wetted to be of much use in water conduction. In sandy soils where southwestern sunflower species thrive, shifting sands frequently pile around lower stalks of plants, where subsequent rainfall may initiate adventitious root growth. For adventitious roots of sunflower to have adaptive value under drought conditions, they must be conductive. Anatomical studies indicate that the internal anatomy of adventitious roots is nearly identical with the anatomy of primary roots for both Hopi (Fig. 4a and 4b) and hybrid 894 (Fig. 4c and 4d); hence, they should function in the conduction of water (Esau, 1965). However, serial sectioning indicated that primary roots and especially the adventitious roots of hybrid 894 have large air spaces in their cortex. Secondary growth in the adventitious roots of hybrid 894 via the vascular cambium favors a greater production of woody xylem in relation to the quantity of cortical parenchyma that is produced. Xylem expansion is compensated in the cortex by large cells flattened circumferentially (Fig. 4c), or by a combination of flattened cells and larger intercellular spaces (Fig. 4d). However, the growth characteristics of xylem and cortex in Hopi roots result in a more compact cortex of isodiametric cells (Fig. 4a and 4b). Plant root characteristics can be modified through breeding and selection independently of aboveground characteristics (Taylor and Klepper, 1978). This may have hap-

pened during the history of developing advanced hybrid varieties of sunflower, where maximum seed production becomes more important to varietal survival than additional root development of mature plants. Development of cultivars of sunflower with greater capacity for producing conductive adventitious roots could possibly enhance their drought resistance in dryland farming where soil may be "thrown" around plant bases during routine cultivations.

Another adaptive function for adventitious roots in sunflower might be increased anchorage for large plants. Wild plants with radiating roots in shifting, sandy soil would undoubtedly have greater stability than plants lacking such roots. Under cultivated conditions, lodging due to wind can be a serious problem for sunflower standing in wet soil, especially where heads are heavy with maturing seed. It is conceivable that cultivated hybrids having radiating adventitious roots would be more resistant to uprooting by wind than current hybrids which lack these roots.

In the greenhouse study, Hopi sunflower stalks were significantly more resistant to deflection by a given horizontal force than were stalks of hybrid 894. This was true whether the force was applied at 0.3 or 0.6 m above the original soil surface. For brevity, stalk deflections at the 0.3-m height caused by horizontal forces of 0.9 and 1.8 kg are reported. The association of stalk deflection and added soil around the base of the plant was significant for both hybrid 894 and Hopi sunflower (Table 2). None of the stalk or root factors that were measured had any significant effect on deflection in hybrid 894. Deflections in Hopi at the 0.3-m height were significantly associated with stalk diameter (5% level), dry weight of primary roots (5% level), and dry weight of adventitious roots (1% level). The multiple linear regression indicated that the greater resistance in Hopi to deflection by horizontal forces of 0.9 and 1.8 kg was due to its rooting characteristics, with the adventitious roots contributing the greatest influence on stability. Based on our results, we anticipate that the development of hybrid sunflower with the adventitious rooting characteristic may result in

cultivars having greater resistance to lodging due to wind than currently exists.

An additional benefit that might be realized by developing hybrid sunflower possessing the adventitious rooting characteristic could be reduced susceptibility to injury by insect larvae burrowing in the primary roots. The vascular systems of primary roots of cultivated sunflower are frequently severely injured by larvae of *Eucosma womonana* Kearfott (Rogers et al., 1979), *Cylindrocopturus adspersus* (LeConte) (Rogers and Jones, 1979), and *Baris strenua* (LeConte) (Oseto, 1977). Plants infested by these insects often lodge or exhibit symptoms resembling severe drought stress. Plants capable of producing adventitious roots above the injury sites of these insects might be able to withstand the deleterious effects of their infestation better than current hybrids. Controlled studies on the contribution of adventitious roots to survival of sunflower with damaged primary roots seems warranted.

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